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THE FERN-LEAVED MONKEYFLOWER (PHRYMACEAE), A NEW SPECIES FROM THE NORTHERN SIERRA NEVADA OF CALIFORNIA

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ABSTRACT

The fern-leaved monkeyflower, **Mimulus filicifolius** (Phrymaceae, Section *Simiolus*), is a new species described from the northwestern corner of the Sierra Nevada of California. The new taxon is differentiated from close relatives of *Mimulus* L. (*M. laciniatus* Gray and *M. guttatus* DC.) mostly by having many finely divided, bi-pinnately compound leaves. **Mimulus filicifolius** occurs mainly within ephemeral seeps of rock outcrops, where it occupies similar habitats to *M. laciniatus*, which occurs farther south in the Sierra Nevada. **Mimulus filicifolius** appears to be highly geographically restricted, and is currently known only from Butte and Plumas Counties within the Plumas National Forest. It therefore merits strong conservation consideration.

Key Words: California, compound leaves, fern-leaved monkeyflower, *Mimulus*, *Mimulus guttatus*, *Mimulus laciniatus*, Plumas National Forest.

The genus *Mimulus* L. (Phrymaceae) is a diverse plant group that has its center of diversity in western North America (Grant 1924). Within this group, section *Simiolus* contains a variety of species that inhabit a wide array of habitats, from coastal areas to high mountains, and has become a focal group of interest in ecological and evolutionary studies (Wu et al. 2007). Within section *Simiolus*, the *Mimulus guttatus* DC. species complex comprises a group of morphologically differentiated, yet often interfertile species (Vickery 1964). Here we describe a new species that is distinguished within section *Simiolus* mainly by having finely divided leaves, specimens of which were previously determined as *Mimulus laciniatus* A. Gray.

Species having divided leaves and leaf margins are rare within the genus *Mimulus*. *Mimulus guttatus* can have toothed margins, especially near the leaf base (Grant 1924), yet leaves of *M. guttatus* are mostly entire. Section *Simiolus* specimens having very finely divided leaves have been collected in and near Plumas National Forest since 1974 (CA S871913). *Mimulus laciniatus* was previously the only known member of *Mimulus* to have strongly dissected leaf margins (Grant 1924; Thompson 2012). *Mimulus laciniatus* is an annual plant endemic to the central western slope of the California Sierra Nevada where it primarily occupies ephemeral granite seeps at elevations generally >900 m (Sexton et al. 2011). *Mimulus laciniatus* leaf divisions extend throughout the leaf, forming a laciniate or pinnately compound shape. The *M. laciniatus* species range is found between Tulare and Amador counties from south to north, respectively, but the morphologically distinct taxon described here (previously described as *M. laciniatus*) occurs approximately 150 kilometers north of the nearest known populations of *M. laciniatus* (Fig. 1).

Butte and Plumas County specimens, previously determined as *M. laciniatus*, differ morphologically from *M. laciniatus* mainly by having leaves that are finely twice-pinnately compound and having more primary leaf divisions, giving the leaves a delicate, fern-like appearance. Molecular genetic analyses indicate that the Butte Co. subpopulation from which the type specimen described here originates is genetically distinct from the *M. laciniatus* clade, and reproductive barriers in the form of hybrid sterility exist between this subpopulation and *M. laciniatus* and *M. guttatus* populations (Ferris et al., unpublished data). First-generation hybrids between individuals from this new taxon and *M. guttatus* and *M. laciniatus* individuals exhibited hybrid sterility, whereas there is no comparable barrier between the same *M. laciniatus* and *M. guttatus* individuals. The above evidence of

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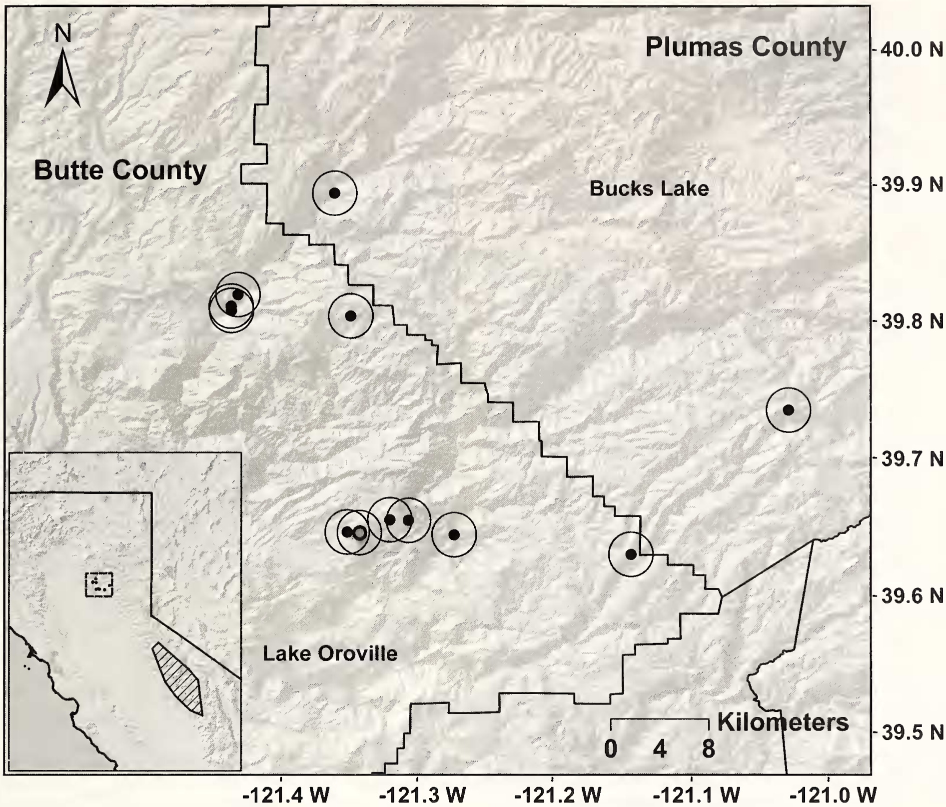

FIG. 1. Species distribution of known *Mimulus filicifolius* locales within Butte and Plumas Counties (dashed-line box within map inset), of the northwestern Sierra Nevada of California. The open circle represents the location of the *M. filicifolius* type specimen at Big Bald Rock (39°38′39″N, 121°20′36″W). The species range of the morphologically similar *Mimulus laciniatus* in the central Sierra Nevada is shown as the polygon with diagonal lines in the map inset.

strongly differing morphological characters, reproductive barriers, and evidence of divergent evolution leads us to conclude that the northern Sierran plants previously identified as *M. laciniatus* should be treated as a distinct species.

Taxonomic Treatment

Mimulus filicifolius J. P. Sexton, K. G. Ferris & S. E. Schoenig, sp. nov.—TYPE: USA, California: Butte County, granite seeps of easterly area of Big Bald Rock, 39°38′39″N, 121°20′36″W, ca. 930 m elev., 22 May 2010, *J. P. Sexton 1* (holotype, DAV). Figures 2 and 3.

Herbaceous annual, 3–38 cm, glabrous throughout. **Leaf petioles** 0–32 mm, **leaf blade** 3–68 mm, oblanceolate to ± ovate, bi-pinnately, narrowly to finely lobed (linear) or dissected, often having >8 primary pinnae divisions on a side. **Inflorescence** a raceme, generally >5-fld; bracts clasping at base, entire, ovate. **Flowers** open, occasionally cleistogamous; **pedicel** 2.5–14 mm; **calyx** 2–11 mm, strongly curved (rounded), asymmetrically swollen in fruiting, ± glabrous, lobes unequal, lowest 2 upcurved in fruiting; **corolla** pale yellow, tube-throat 4–8 mm; **placentas** axile. **Fruit** 3–8 mm, ovoid to fusiform, loculicidal (indehiscent), chambers 1–2; **seeds** many, generally <1 mm, ovoid, ± yellow to dark brown.

Mimulus filicifolius is distinguished from *M. laciniatus* by having strongly bi-pinnately and finely divided—often linear—leaf margins in larger plants, and more primary leaf divisions (often having 8 or more primary leaf divisions on one leaf side) (Figs. 4, 5), as opposed to having mostly laciniate to occasionally bi-pinnate leaf shapes (with 7 or less primary leaf divisions on one leaf side, often 3 or less) with oblanceolate lobes; having clasping, entire, ovate floral node bracts, as opposed to having bract bases long-tapered to petioled, and bracts narrowly lanceolate to pinnately lobed; and having pedicels less than 2 times the calyx length, as opposed to often having pedicels equal to 2 times the calyx length or longer (Table 1, Fig. 5).

Paratypes

We examined all of the known herbarium specimens of *M. filicifolius*, including paratypes

FIG. 2. *Mimulus filicifolius* prior to flowering, growing near Feather Falls, Butte Co., California, 12 May 2012. Photo by S. Schoenig.

(Table 2). The following paratypes (herbarium and specimen codes are given in parentheses) are from the *M. filicifolius* geographic range and were previously identified as *M. laciniatus*: USA. CALIFORNIA. **Butte Co.:** South of Lumpkin Ridge, 12 May 1987, *L. Ahart 5634* (CAS 916469,

FIG. 3. *Mimulus filicifolius* flowering at basalt site south of Lumpkin Ridge, Butte Co., California. Photo by Robert Schlising.

FIG. 4. *Mimulus filicifolius* leaves from plants growing at Big Bald Rock, Butte Co., California. Photograph by S. Schoenig. Scale bar = 5 mm.

CHSC 42866); Fall River at the head of Feather Falls, 30 April 1990, V. *Oswald 4175* (CHSC 50115); along Bean Creek Rd near Little Bald Rock, 22 May 1985, *L. Ahart 5027* (CHSC 40889), 7 June 2009, *D. Grossenbacher and M. James 1032-a* (DAV 189651); Big Bald Rock, 14 June 1980, *R. Banchero 220* (CAS 871914, CHSC 33342); Bald Rock Dome, 15 May 1983, R. *Schlising 4414* (CHSC 39058); between Pulga and Poe Dam near the North Fork of the Feather River, 11 September 2006, *L. Ahart 13,293* (CHSC 94564); Poe Dam area, 26 April 1986, V. *Oswald 1981* (CHSC 49002). **Plumas Co.:** North Fork Feather River 1/2 mile below the mouth of Rock Creek, between Storrie and Elephant Butte Tunnels, 28 April 1974, *W. Dakan* (CAS 871913).

Additionally, three locales of *M. filicifolius* that are awaiting accession or have not yet been collected include the following: **Butte Co.:** Poe Dam area, along Camp Creek Road at crossing of Dogwood Creek, 21 May 2013, *L. Janeway 11,114* (awaiting accession); Rody Creek, 4 October 2012, *T. Hanson and M. Williams* (not collected). **Plumas Co.:** Northeast end of Lumpkin Ridge, 21 May 2013, *T. Hanson* (awaiting accession).

Morphological Analysis

We quantified differences in leaf shape and pedicel length between *M. filicifolius* and *M. laciniatus* from herbarium specimens. Analyses included nine locales (of 12 known) of *M. filicifolius* from Butte and Plumas counties, and

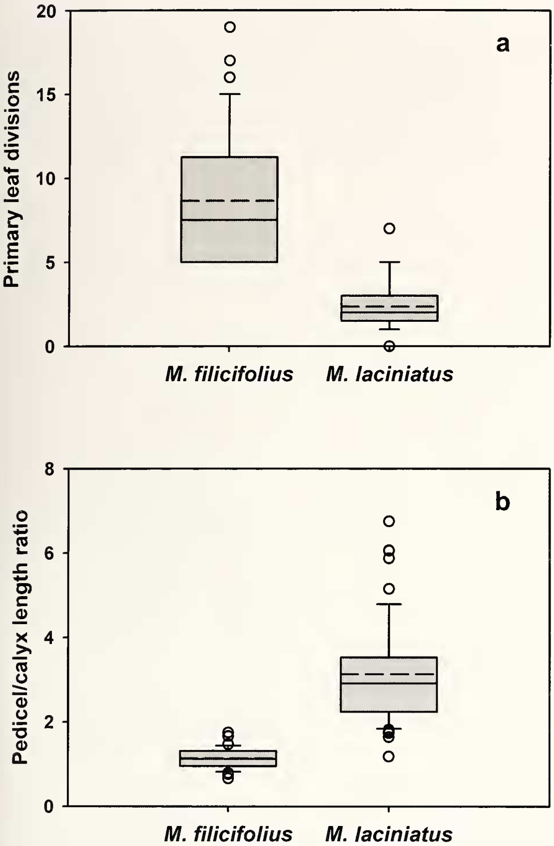

FIG. 5. Box plots of morphological data of distinguishing characters between *Mimulus filicifolius* and *Mimulus laciniatus*. (a) Number of primary leaf divisions (range = 5–19 and 0–7 for *M. filicifolius* and *M. laciniatus*, respectively). (b) Pedicel/calyx length ratio (range = 0.667–1.75 and 1.19–6.75 for *M. filicifolius* and *M. laciniatus*, respectively). Box boundaries are 25th and 75th percentiles. Dashed centerline is the mean; unbroken centerline is the median. Whiskers are 90th and10th percentiles. Unfilled circles are points outlying.

12 locales from four counties representing much of the species range of *M. laciniatus* (Table 2). We recorded data from each plant having clearly observable traits on a herbarium collection sheet (Table 2). Only complete individuals (i.e., having attached roots or being the only specimen on a sheet) were counted. For leaf shape, we recorded the greatest number of primary divisions on one side of the longest leaf on a plant. Leaf margin lobes near the leaf tip were included in counts since it was difficult to distinguish primary and secondary pinnae there. A total of 34 and 57 individuals were measured for leaf shape in *M. filicifolius* and *M. laciniatus*, respectively. For pedicel length, we measured the longest pedicel and its associated calyx on a given plant and recorded the pedicel/calyx length ratio. We measured a total of 36 and 73 individuals for pedicel/calyx length ratios for *M. filicifolius* and *M. laciniatus*, respectively.

Morphological data were analyzed using REML (JMP, version Pro 10). The effect of species was considered a fixed factor, whereas population (locale) was considered a random factor nested within species since we were primarily interested in species differences. Species differences were highly significant for both leaf and pedicel traits. For leaf shape, *M. filicifolius* and *M. laciniatus* had least square means of 8.23 (±0.78 SE) and 2.52 (±0.65 SE) primary pinnae, respectively (df = 1; error df = 17.29; $F = 31.75$; $P < 0.0001$; Fig. 5a). For pedicel length, *M. filicifolius* and *M. laciniatus* had least square means of 1.15 (±0.32 SE) and 3.23 (±0.24 SE) pedicel/calyx length ratios, respectively (df = 1; error df = 16.89; $F = 26.91$; $P < 0.0001$; Fig. 5).

Distribution and Habitat

The epithet ('fern-leaved' in Latin) for the new species refers to its strong and finely compound leaf structure (Figs. 2–4). *Mimulus filicifolius* is known between 430–1280 m within the Feather River watershed of the northern California Sierra Nevada (Fig. 1) and most specimens are known from slow-draining, ephemeral seeps of the Bald Rock Pluton in Butte County (e.g., Big Bald Rock, Little Bald Rock, and Bald Rock Dome), with noted exceptions (e.g., localities on Lovejoy basalt at Lumpkin Ridge). These habitats are mainly comprised of exfoliating granite slabs on which mosses and club mosses grow and occur within a mixture of chaparral and yellow pine forest, dominated by *Arctostaphylos viscida* Parry, *Quercus chrysolepis* Liebm., *Quercus kelloggii* Newb., *Pinus ponderosa* ex Lawson and C. Lawson, and *Pseudotsuga menziesii* (Mirb.) Franco. Noted native plant associates of *M.*

TABLE 1. DIAGNOSTIC MORPHOLOGICAL CHARACTERS BETWEEN *MIMULUS FILICIFOLIUS* AND *M. LACINIATUS*.

Trait	*M. filicifolius*	*M. laciniatus*
Leaf shape	pinnate to strongly bi-pinnate, having fine, linear lobes; often having 8 or more primary pinnae on a side	laciniate to bi-pinnate, lobes oblanceolate, ≤7 primary pinnae on a side and often having 3 or less.
Floral bracts	clasping, ovate, entire	base long-tapered to petioled, lanceolate to pinnately lobed
Pedicels	relatively short, <2 times calyx length	relatively long, often ≥2 times calyx length

TABLE 2. SUMMARY INFORMATION FOR THE 12 KNOWN LOCALES OF *MIMULUS FILICIFOLIUS* AND 12 LOCALES OF *MIMULUS LACINIATUS* TO WHICH MORPHOLOGICAL CHARACTERS WERE COMPARED. Leaf shape and pedicel/calyx length ratio data were recorded from herbarium sheets. Herbarium code and specimen number are given in the Specimen ID column and the number of individual plants examined from each herbarium sheet for each trait is given in subsequent columns. CAS = California Academy of Sciences; CHSC = Chico State Herbarium, California State University, Chico; DAV = University of California, Davis Center for Plant Diversity; JEPS = Jepson Herbarium. Additionally, three records of *M. filicifolius* that have not yet been accessioned or collected are listed (NA).

Specimen ID	Species	Locale	*N* (leaf)	*N* (pedicel)	Lat.	Long.
CHSC 39058	*M. filicifolius*	Bald Rock Dome, Butte Co., CA, USA	6	9	39.6536	−121.3067
CHSC 40889, DAV 189651	*M. filicifolius*	Bean Creek Road, near Little Bald Rock, Butte Co., CA, USA	4	4	39.6539	−121.3203
CAS 871914, CHSC 33342	*M. filicifolius*	Big Bald Rock, Butte Co., CA, USA	2	2	39.6450	−121.3517
DAV 190412, DAV 190658, DAV 190659	*M. filicifolius*	Big Bald Rock, Butte Co., CA, USA	4	5	39.6445	−121.3427
CHSC 50115	*M. filicifolius*	Feather Falls Trail, Butte Co., CA, USA	4	3	39.6431	−121.2731
CA S916469, CHSC 42866	*M. filicifolius*	Lumpkin Ridge, Butte Co., CA, USA	9	8	39.6286	−121.1436
CHSC 94564	*M. filicifolius*	Poe Dam area, Feather River, Butte Co., CA, USA	1	1	39.8072	−121.4367
CHSC 49002	*M. filicifolius*	Western Pacific Railroad between Pulga and Poe Dam, Butte Co., CA, USA	2	2	39.8106	−121.4369
NA	*M. filicifolius*	Poe Dam area, along Camp Creek Road at crossing of Dogwood Creek, Butte Co., CA, USA	NA	NA	39.8189	−121.4319
NA	*M. filicifolius*	Rody Creek, Butte Co., CA, USA	NA	NA	39.8032	−121.3490
CAS 871913	*M. filicifolius*	North Fork Feather River, Plumas Co., CA, USA	2	2	39.8933	−121.3610
NA	*M. filicifolius*	Northeast end of Lumpkin Ridge, Plumas Co., CA, USA	NA	NA	39.7342	−121.0278
JEPS 10456	*M. laciniatus*	Yosemite National Park, Mariposa Co., CA, USA	—	4	—	—
JEPS 10937	*M. laciniatus*	Hog Ranch, Tuolumne Co., CA, USA	6	7	37.8822	−119.8547
JEPS 10938	*M. laciniatus*	Dardanelle, Tuolumne Co., CA, USA	5	7	38.3411	−119.8328
JEPS 11022	*M. laciniatus*	Yosemite Falls, Mariposa Co., CA, USA	1	7	—	—
JEPS 11025	*M. laciniatus*	Strawberry Lake, Tuolumne Co., CA, USA	4	6	38.1954	−119.9808
JEPS 11026	*M. laciniatus*	Marble Fork, Sequoia NP, Tulare Co., CA, USA	1	2	36.5534	−118.8102
JEPS 23793	*M. laciniatus*	Jose Basin, Fresno Co., CA, USA	9	9	37.1014	−119.3738
JEPS 33899	*M. laciniatus*	Mono Hot Springs Campground, Fresno Co., CA, USA	8	9	37.3267	−119.0167
JEPS 53950	*M. laciniatus*	Vermillion Valley, Fresno Co., CA, USA	9	7	37.4081	−118.9383
JEPS 55430	*M. laciniatus*	Miramonte, Fresno Co., CA, USA	3	3	36.6925	−119.0514
JEPS 6975	*M. laciniatus*	Mills Creek, Fresno Co., CA, USA	7	8	37.4244	−118.8578
JEPS 82859	*M. laciniatus*	Clover Creek, Tulare Co., CA, USA	4	4	36.6019	−118.7428

filicifolius at Big Bald Rock include species of *Bryum* Sendtn. ex C. Müll., *Cheilanthes gracillima* D. C. Eaton, *Heterocodon rariflorum* Nutt., *Penstemon newberryi* A. Gray, and *Selaginella wallacei* Hieron. Flowering specimens of *Mimulus filicifolius* have mostly been collected or observed from April to June, with one specimen collected in September (L. Ahart 13293, CHSC 94564).

Conservation Considerations

Mimulus filicifolius is endemic to the northwestern corner of the California Sierra Nevada and is known from only 12 locales on or adjacent to the Plumas National Forest, several of which are closely spaced (Fig. 1). We did not perform extensive searches to locate new populations within suitable habitat. Besides Big Bald Rock, the type specimen locale, we visited several other locales from 2006 to 2012 to observe habitats and the range of phenotypes from several sites across the species range. The locale visited at Big Bald Rock appeared to be healthy (containing thousands of individuals). Nevertheless, we were unable to locate plants at the paratype locales near Pulga and Poe Dam near the North Fork of the Feather River from which specimens had been collected by *L. Ahart 13,293* (CHSC 94564) and *V. Oswald 1981* (CHSC 49002). L. Ahart described the population at this locality as "uncommon, only one plant seen." However, a new locale nearby was recorded by Lawrence Janeway (collection number 11114) in 2013, confirming that plants still occur in this area. Additionally, at the paratype collection site near Little Bald Rock, *M. filicifolius* was described as "uncommon," although we did not visit this locale. The population that we observed at Feather Falls Trail was fairly small, consisting of perhaps a few dozen individuals adjacent to a scenic overlook. Since there are few known populations, some of which are small and occur close to each other, we recommend that conservation managers include this species in monitoring programs to limit future risks to existing populations (e.g., species invasions, land clearing, livestock introductions). Additionally, suitable habitats within the region should be searched in case other populations exist.

Discussion

We find no evidence that *Mimulus laciniatus* occurs within the species range of *M. filicifolius*. All specimens known from Butte and Plumas counties are consistent with the *M. filicifolius* phenotype and it appears from our analysis that these two taxa are strongly diverged geographically and evolutionarily.

Mimulus filicifolius has a lobed leaf shape similar to, but more finely dissected than, *M. laciniatus*. *Mimulus filicifolius* and *M. laciniatus* also occupy similar habitats—seeps in rocky outcrops. *M. laciniatus* has been shown to be adapted to these habitats compared to its close relative, *M. guttatus* (Peterson et al. 2013). Since *M. filicifolius* is genetically distinct from *M. laciniatus* (Ferris et al., unpublished data) its leaf shape may be an independent derivation of lobed leaves in the genus *Mimulus*, which would represent parallel phenotypic evolution in parallel environmental conditions and thus be strong evidence of adaptation.

A lobed leaf shape may be adaptive in exposed, outcrop environments because it may help reduce heat stress and water loss in the daytime and/or reduce cold stress at night. Rock outcrops are drier, more light-intensive and have more extreme ground temperatures than the longer-lasting seep and stream habitats of nearby Simiolus species such as *M. guttatus* or *M. nasutus* (K. Ferris unpublished data). Lobed leaves have thinner boundary layers than round leaves, which increases the efficiency of convective heat transfer. Heat loss through convection can reduce the amount of water lost to evaporative cooling in hot, dry environments like rocky outcrops (Givnish 1978; Schuepp 1993; Nobel 2005; Nicotra et al. 2011).

Lobed leaves may also contribute to freeze tolerance early in the growing season when nights are still cold. On clear nights, leaves in exposed, open areas like *M. filicifolius* and *M. laciniatus* habitats radiate heat to the cold sky. This radiation can cause leaf temperatures to fall below air temperature by several degrees and thus leaves can freeze when air temperatures are near, but still above 0°C (Darwin and Darwin 1880; Nobel 2005). Because of their reduced boundary layer lobed leaves should stay closer to air temperature than round leaves and thus warmer at night. Because of the above physiological effects lobed leaves in *M. filicifolius* and *M. laciniatus* could be a key adaptive trait in the rocky outcrop environments they occupy, although we acknowledge that these hypotheses remain to be rigorously tested.

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